ECOLOGICAL STRATEGIES IN COLLEMBOLA: A NEW APPROACH TO THE USE OF TERRESTRIAL INVERTEBRATES IN ENVIRONMENTAL ASSESSMENT

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ЭКОЛОГИЧЕСКИЕ СТРАТЕГИИ У НОГОХВОСТОК: НОВЫЙ ПОДХОД К ИСПОЛЬЗОВАНИЮ НАЗЕМНЫХ БЕСПОЗВОНОЧНЫХ ДЛЯ ОЦЕНКИ СОСТОЯНИЯ СРЕДЫ

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Application of a three strategy-habitat templet model allows collembolan species to be classified according to their biological characteristics as primarily r-, K- or A - selected. When details of their bionomics are unknown species can be classified according to their micro- and macro-habitats whose properties their biology reflects. On any site the ecological strategies of each of the species present can be placed in one of these three primary categories or in intermediate categories. The relative frequencies or abundances of the species falling into each of these classes can be summed and the totals reduced to a single vector on the habit templet. The magnitude and direction of this vector can then be compared for different sites. In the example described here, grassland sites differed in vegetation status (natural or improved pasture) and in intensity of grazing. Disturbance, that is change away from natural grassland, or increase in grazing pressure, caused movement from K- towards r- selected collembolan species. With the method used here this shift is readily quantified and illustrated graphically.

One task confronting ecologists today is the application of the results of ecological research to environmental assessment, that is to determine and anticipate the effects of man's activities on natural and semi-natural ecosystems. This creates a need for methods by which habitats can be compared using their component biota among which, in terrestrial environments, arthropods comprise the greater part of total biological diversity. Among suitable environmentally sensitive groups of arthropods are the ants /10/ and the Collembola /4/. Here we use data on Collembola from a series of pasture trials in eastern Australia to assess some of the consequences of introducing exotic pasture species and of grazing by sheep.

That organisms show three primary evolutionary responses to properties of habitat has been proposed for plants /5,6/ and animals /1,2,12/. Habitat is described by position on the habitat templet /12/, determined by two coordinates referring to the habitat's predictability and stability, and to its favourableness, an inverse measure of the extent to which it imposes stress.

When properties of a habitat are known, it is possible to predict the relative frequency with which its inhabitants should possess the attributes related to their demography, dispersal abilities, breeding systems and so on which constitute ecological strategies. Alternatively, with information on the bionomics of the species occurring in a habitat, habitat itself can be

characterised. Since one axis of the habitat templet is its stability, the composition of its fauna can provide a quantitative description of the extent to which it has been destabilized, for example by human disturbance.

Sites and Sampling Procedure

Data come from a series of investigations of the soil fauna of pasture near Armidale on the New England Tableland, New South Wales (/8,9/, and included references). A full account of collembolan faunas, emphasising the distributions of native and introduced species, is given in /7/. Soils were gleyed podsols and the area has a mean annual rainfall of 870 mm with average 60% summer incidence. Treatments were set up in 1963 and data used now come from three different years, all of which had close to average annual rainfall.

One set of treatments consisted of floristically diverse natural grassland with the native grasses Themeda australis and Poa sieberana which was grazed up to maximum sustainable carrying capacity at rates of 0. 5 and 10 sheep per hectare. Other treatments involved improved pasture; this was sown with Phalaris aquatica and Trifolium repens, and fertilised with superphosphate. These more productive pastures were stocked at higher rates with 10-12, 20-24 and 30-36 sheep per hectare.

On each site that was studied Collembola were sampled over a year. They were extracted in Tullgren funnels from soil cores, 10 cm diameter by 5 cm deep, after herbage had been trimmed to 5 cm. More than 1.000 cores were extracted, over 100.000 Collembola have been identified to species and sampling intensity appears to have been adequate for the present analysis.

Strategic Allocation of Collembolan Species

A triad of primary selection processes and resultant ecological strategies are recognised which are determined by properties of habitat: r- or exploitation-selection for productivity in temporary, unpredictable habitats; K- or interaction-selection for persistence in predictable, favourable habitats; A- or adversity-selection for conservation of adaptation in predictable but unfavourable habitats. Collembolan species are allocated to these primary categories, or to the intermediate rK, KA or rA strategies at two levels according to their usual macro- and micro-habitats on the basis of familiarity with the natural history of the taxa concerned and from the literature describing other studies of their bionomics. This avoids any circularity arising from the use of biological information from these samples. The first level refers to the broad-scale habitats or vegetation types in which species are most frequently found; the second refers to vertical distributions in and above the soil profile, supported by the evidence of gross morphological adaptations (see below).

At the macro-scale, species occurring in biologically diverse arthropod communities in natural vegetation are classed as K strategists (see legend to Table). Those living in temporary habitats or habitats disturbed and altered by man are classed as r strategists. At this scale A strategists are not represented in these samples. They are found on mountain-tops and in cold forests, caves and the littoral zone on the sea-shore.

Macro- and micro-habitats and inferred strategies of
Armidale pasture Collembola (status: N, native; I, introduced)

Species	Combined		
	Macro-habitats	Micro-habitats	Classi-fication
1	2	3	4
Neanuridae			
Neanura muscorum (Templeton) (I)	1	4,5	r - r K
Australonura meridionalis (Stach) (N)	5	8	K - A
Paleonura sp. (N)	5	5-7	K - K A
Gen. nr Ceratrimeria sp. (N)	5	4-6	K - r K
Brachystomella platensis Najt & Massoud (I)	2	4-6	r - r K
Hypogastruridae			
Hypogastrura denticulata (Bagnall) (I)	1	4,5	r - r K
H. vernalis (Carl) (I)	1	4,5	r - r K
Onychiuridae			
Mesaphorura sp. cf. krausbaueri (Börner) (I)	2	6,7	r - K A
Onychiurus sp. armatus group (Tullberg) (I)	1	6,7	r - K A
Isotomidae			
Cryptopygus thermophilus (Axelson) (I)	1,2	4	r - r
C. australis Womersley (N)	5,6	4,5	K - r
C. caecus Wahlgren (N)	5,6	6	K - K
Folsomides exiguus Folsom (N)	5	5,6	K - K
Isotomodes productus (Axelson) (I)	2	7	r - A
Proisotoma filifera Denis (I)	2	4	r - r
Isotoma notabilis Schäffer (I)	2	5,6	r - K
Isotomiella minor (Schäffer) (N)	5-7	4-7	K - r A
Folsomia candida (Willem) (I)	2,4	6,7	r - K A
Entomobryidae			
Australotomurus barbatus Mari Mutt & Greenslade (N)	6	1	K - K
Sinella sp. termitum group Schött (N)	2,5,7	9	r K - A
Lepidocyrtoides sp. (N)	5,6	4	K - A
Acrocyrtus sp. of ralumensis Schäffer (N)	5	4,5	K - r K
Drepanura cinquilineata Womersley (N)	7	1	K - K
Entomobrya multifasciata (Tullberg) (I)	1,2	4	r - r
E. nivalis (Linne) (I)	2	4	r - r
E. nicoleti (Lubbock) (I)	2	4	r - r
E. unostrigata Stach (I)	1,2	4	r - r
Metacoelura articulata (Schött) (N)	7	1	K - K
Neelidae			
Megalothorax sp. (N)	5-7	7	K - A

(End)

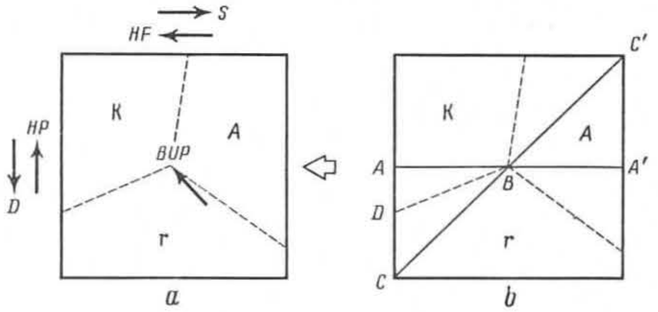
1	2	3	4
Sminthuridae			
Sminthurinus sp. tuberculatus group Delamar & Massoud (N)	2,3,9	4,5	r K - r K
Sminthurinus sp. (N)	6	4,5	K - r K
Arrhopalites caecus (Tullberg) (I)	1,3	6,7	r - K A
Gen. nr Parakatianna sp. (N)	6	5,6	K - r K
Katianna oceanica var schoetti Womersley (N)	2,7	1	r K - K
Polykatianna aurea (Womersley) (N)	6	2	K - K
Sminthurides sp. (N)	7,8	10	K - A
Sphaeridia pumilis Krausbauer (I)	2,7	4	r K - r
Bourletiella viridescens Stach (I)	2	3	r - K
Rastriopes sp. (N)	6	2	K - K
Corynephoria sp. 1 (N)	7	1	K - K
Corynephoria sp. 2 (N)	7	1	K - K

N o t e s: Macro-habitats: 1 - open, disturbed sites; 2 - exotic grasslands and improved pastures; 3 - other non-native vegetation; 4 - urban areas; 5-9 - native vegetation: 5 - forests; 6 - woodlands; 7 - grasslands; 8 - wetlands; 9 - other. Micro-habitats: 1 - grasses and/or sedges; 2-heathy vegetation; 3 - other plants; 4 - leaf litter; 5 - humus; 6 - upper soil profile; 7 - lower soil profile; 8 - logs; 9 - ant and termite nests; 10 - water surfaces.

At the micro-scale, species living on vegetation and in humus and the species-rich upper part of the soil profile are treated as K strategists. Species colonising surface litter are r strategists /3/ and inhabitants of old decaying logs or lower, mineral horizons in the soil are A strategists. At this scale extreme A strategists have reduced body pigment, ocelli and appendages, and typically they lack a jumping organ while the r strategists of the litter layer are pigmented, have 8 + 8 ocelli, longer legs and antennas, and possess a jumping organ.

Results and Discussion

The collembolan species recorded in these trials, their chief habitats and inferred ecological strategies are listed in Table. This is a first attempt and in the future we intend to carry out a more critical examination of this approach to environmental assessment. No doubt Table will be improved upon as further information becomes available, and some allocations need discussion which space now prohibits. It is unlikely, however, that further work will materially affect our conclusions here.



F i g. 1. The habitat templet

a) HF - habitat favourableness; S - intensity of stress; HP - habitat predictability (durational stability, heterogenety in space at one time); D - intensity of disturbance; BUP - biotic unpredictability, impact of biotic interactions.

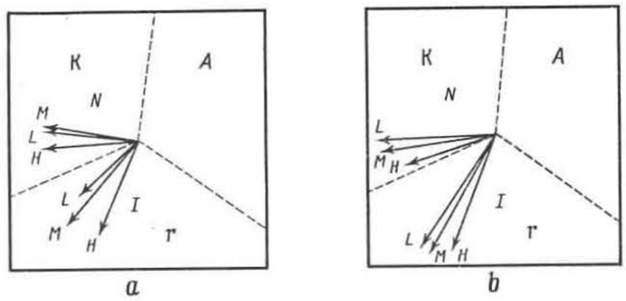
b) Delineation of areas dominated by r -, K -, A - selection processess. Let r - selection operate below the line AA' (low habitat predictability), and K - selection above and to the left of the line CC' (high biotic unpredictability). The rK boundary is the line BD bisecting the angle ABC. The KA and rA boundaries are then fixed at angles of 120° and 240° from the BD, rK boundary

Secondary, intermediate strategies are partitioned between primary strategies and totals are summed, first for the two levels of habitat for each species, then for all the species recorded from each treatment (qualitative data), and finally for all individuals from each treatment (quantitative data). This gives proportional distributions of strategies which are shown as single vectors on the habitat templet.

For this purpose it is necessary to divide the habitat templet into discreate r-, K- and A- dominated areas (Fig.1), although it must be emphasised that habitats do not fall into such neatly bounded classes. Instead, the habitat templet should be regarded as indicating areas (habitats) which predict the frequency with which certain attributes of species (strategies) will or will not be encountered .

With this proviso, it is clear from Fig.2 that there are pronounced differences between the natural and improved pastures, and lesser differences that can be ascribed to intensity of grazing. In both cases strategies rotate from K- towards r- selection; this is shown by qualitative and by quantitative data.

The lowest or highest stocking rates on each type of pasture (i.e. equivalent grazing pressures), or similar stocking rates, the intermediate on the natural and the lowest on the improved pasture (i.e. equal grazing pressures) can be compared to assess the effect of pasture improvement alone. Fig. 2



F i g. 2. Strategic responses of Collembola to differencies in type of pasture (N - natural, I - improved) and grazing intensity (L - low, M - medium, H - high) expressed as vectors on the habitat templet; see Fig.1.

Grazing intensities: natural pasture, L, M, H, 0, 5, 10 sheep per hectare; improved pasture, L, M, H, 10-12, 20-24, 30-36 sheep per hectare respectively; a - qualitative data; b - quantitative data

shows how this far outweights effects of grazing, i.e. the differences within each type of pasture.

A greater swing towards r-selected species in the quantitative than the qualitative data can be related to a switch from mainly native Collembola in the natural pasture to a large proportion of individuals of introduced, exotic species in the improved pasture /7/. From Table the ratios of r-K-A strategists amongst native and introduced Collembola are respectively .11-.78-.11 (native species) and .72-.19-.09 (introduced species). The move to r-selection when abundances rather than presence-absence data are considered can be seen to reflect the capacity of populations of r-selected species to grow rapidly and reach high densities in faunas whose diversity and community structure have been modified by man.

Conclusions

Fig.2. demonstrates the usefulness of a simple method based on a current ecological theory that integrates quantitative, faunistic and other biological data to measure and display the effects of disturbance. Further, it points to the potential value of invertebrates, especially Collembola, in the environmental field and to the importance of indentifying fauna to species level. Collembola are abundant and ubiquitous in and on the soil from polar regions to hot deserts and tropical rain-forests, both in natural climax vegetation and in disturbed habitats. In Australia at least there is the additional factor of an introduced, predominantly r-selected element in the collembolan fauna that is closely associated with Matthews' "culture steppe" /11/. Finally, Fig. 2(a) suggests that for comparative purposes a

relatively easily obtained list of species can be as informative as quantitative estimates of population densities.

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Discussion

Petersen H.: I think that you have demonstrated a very useful way to synthesize complex data of animal communities for comparisons between sites. The greatest difficulty seems to be the classification of the individual species Could you tell me how you for instance classify eurytopic species. Do you believe that a generally valid classification could be agreed upon?

Grenslade P.: The classification we used was based solely on distribution records for each species within Australia being mainly corrected by ourselves. Since we obtained a pattern that might have been predicted using this data we were reinforced in our opinion that the classification was a reasonable one. It should be possible to produce a generally accepted classification for all species of Collembola in Australia but it is probably only possible to classify taxa with which one is very familiar. Eurytopic species were classified in various ways, depending on their position in the soil profile.